Emergent properties in the behaviour of a virtual spider robot

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Using a virtual spider robot, we studied hypotheses about the weaving behaviour of orb spiders. Our model spiders built virtual webs that mimicked perfectly the visual architecture of real webs of the garden cross spider *Araneus diadematus*. The matching of capture spiral and auxiliary spiral pitch was an apparently emergent property in both types of web. This validated our interpretation of the garden spider's web-building decision rules, which use strictly local interactions with previously placed threads to generate global architecture.

Keywords: web spider; behaviour modelling; emergent properties; virtual robot

1. INTRODUCTION

The spider's web is a complex structure. It consists of a variety of components hierarchically placed by the animal in a series of modal action patterns (Vollrath 1992). In nature as in technology, complexity often contains specific properties or assemblage patterns—typically called emergent properties—which cannot be inferred analytically from investigations of only the individual components of a system. Thus, repeated interactions between independent units and their environment based on simple local rules often induce high levels of organization and complex arrangements. In biology, simple rules are known to be more robust than complicated rules (Axelrod & Hamilton 1981). Moreover, they are more easily combined and adapted to one another allowing even highly integrated systems to be readily altered.

An excellent example for this phenomenon can be found in spider web-building, a fleeting behaviour that interacts with a growing network of silken threads. A spider such as the common garden spider, *Araneus diadematus*, builds its orb web by first laying radiating spokes and encompassing frame threads. A temporary scaffolding spiral linking the radii is laid from the inside out. It is superseded (and cut down in the process) by the permanent sticky capture spiral laid from the outside in. A final hub adjustment tunes the stays and completes the sticky net that now surrounds and supports the hunter on its aerial perch. The final web, with its evolution into many complex forms (Vollrath 1988), suggests construction principles that are based on the interaction of many simple rules rather than a few very complex rules. If so, it would expect to find emergent properties. The nature of these properties, if we can identify them, would validate our understanding of the rules themselves. This great benefit of emergent properties has been investigated and exploited in several studies in a variety of disciplines, ranging from computer science (e.g. Kauffman 1984; Gibet & Marteau 1994; Campbell & Wang 1996), chemistry (e.g. Aguda 1996) and neurosciences (e.g. Petersen 1988; White *et al*. 1992; Taga 1995), to ecology (e.g. Bossel 1992; Kawata 1995; Harding & Lovelock 1996).

Independently from outlined considerations regarding emergent properties, we created a computer model to investigate the highly interactive but strictly local web-building rules of orb-web spiders. Indeed, the process of orb-web construction is perfectly suitable for modelling, since it can be reasonably simplified as a two-dimensional and geometrical task, which takes place in a well-defined space. Former studies using computers to model web-building (Eberhard 1969; Gotts & Vollrath 1991, 1992; Miranker *et al*. 1992) were not rigorously validated by comparative analyses and their results were stimulating but ambiguous. Our own studies culminated in the virtual spider robot *Theseus*, which mimics the decision processes (as well as some anatomical features) of the garden cross spider *Araneus diadematus*. The main goal of this approach was to provide a tool for hypotheses testing in the context of artificial ethology by continuous cycling of (i) model implementation, (ii) verification against the real animal, and (iii) modification of the rules (Gotts & Vollrath 1991). This iterative process guides the focus of otherwise traditional ethological research by constant comparison of model and original. It quickly pin-points missing, false or ambiguous variables in our hypotheses, and the implementation in object-orientated programming allows for transparent verification and easy modification of the model. The latest version of our model builds virtual webs with realistic properties of real webs; we demonstrated this in previous studies (Krink & Vollrath 1997, 1998*a,b*).

To achieve more powerful evidence for the quality of our latest model, we searched for typical emergent properties in webs built by *Araneus diadematus* and *Theseus*. We found one such property in the coiling pattern of the two
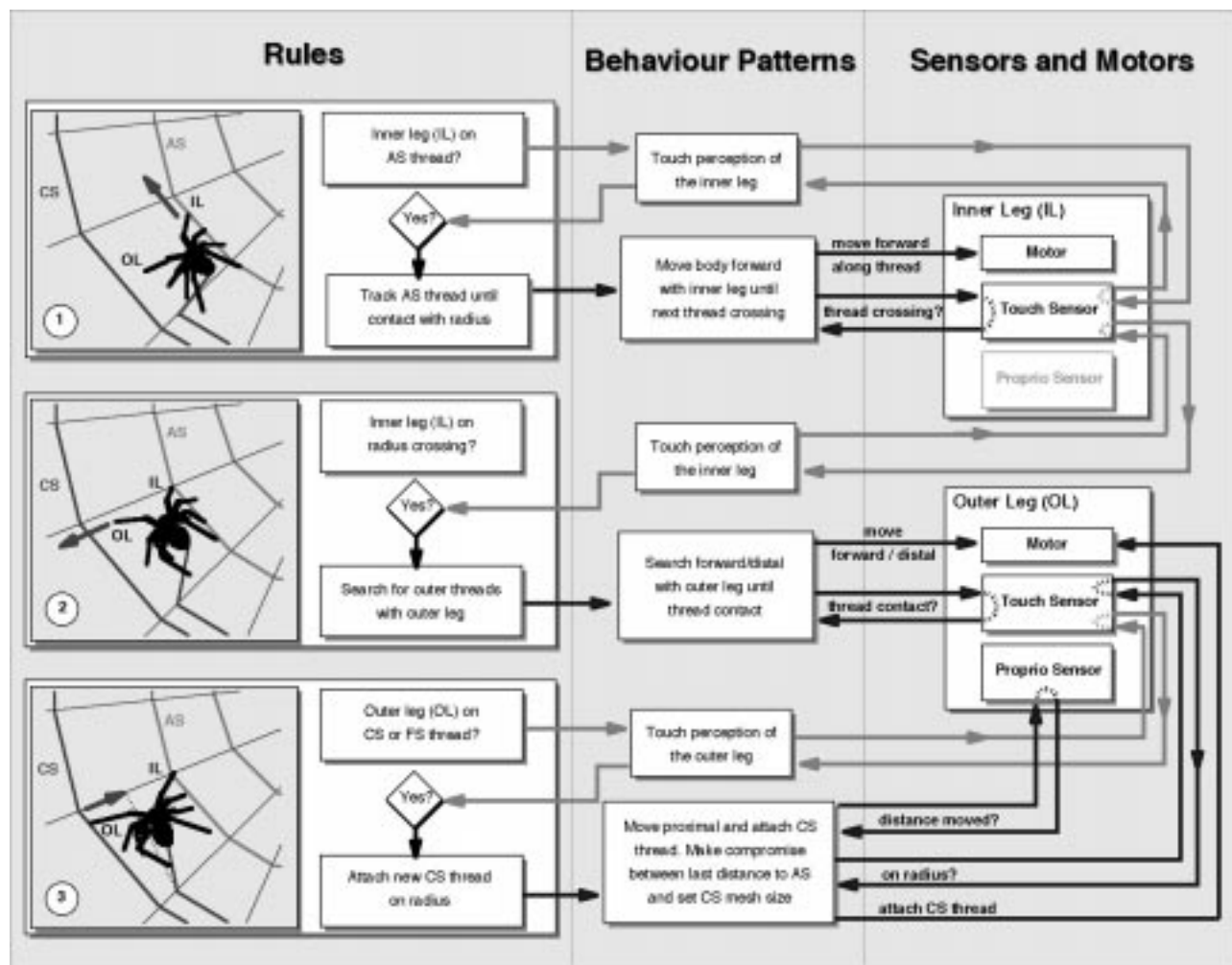
Figure 1. Construction of a cyber thread. The schema shows the effects of three basic rules on the construction of a capture spiral (CS) thread. Each rule consists of a precondition (upper box) and an action (lower box). The directions of the arrows represent the activity flow. Each rule activation and execution starts with a query to the sensory system (grey arrows) and results in the execution of a behaviour pattern that performs a conditional activity loop (black arrows). The first rule (1) directs the spider along the auxiliary spiral (AS) with its inner leg (IL) to the next crossing with a radius. Afterwards, the second rule (2) makes the spider search for outer frame threads and previously constructed CS threads with its outer leg (OL). When the spider finally grasps a thread or stretches its outer leg entirely (3), it attaches a new CS thread on the previously detected radius. The location of the new attachment point is determined by a compromise between the previous distance between the AS and the last CS turn as well as the spider's anticipated mesh size of the CS.

spirals in the web, the temporary scaffolding or auxiliary spiral (AS) and the enduring capture spiral (CS). During construction of the CS, *A. diadematus* seems to use the previously constructed AS as a guideline for spatial orientation (Zschokke 1993). On its way from the periphery to the centre of the web, the spider reverses the direction of its path a few times, while it builds the tightly spaced CS. Owing to these reverses, the spider either follows the coiling direction of the AS or moves in the counter direction. Thus, the percentage of equal coiling of AS and CS (matched coiling) depends upon the number and sequence of reverses during the construction of the CS. Characteristically, *A. diadematus* builds webs with a high percentage of matched coiling; this is interesting because the spider produces this pattern consistently and, we assume, based only on local decisions for path reverses. Thus, if the behaviour of our virtual spider robot is based on valid hypotheses, we would expect to find very similar properties in its virtual webs.

2. MATERIAL AND METHODS

To obtain control webs for our experiments, we kept seven immature *Araneus diadematus* in the laboratory, and photographed and digitized one web of each spider (Vollrath *et al.* 1997). *Theseus'* task was to correctly complete these digitized *Araneus'* webs presented at a stage when radii and AS are in place and the spider positions the CS.

On its way, *Theseus* collected local information in its virtual environment of lines (representing web threads) using touch contact of feet; body and feet positions were monitored using the posture of the segmented legs. New virtual threads were laid down and the old ones rearranged according to the commands of a rule-based controller that activated leg motors by calling specific behaviour patterns. The rules and behaviour patterns that controlled *Theseus'* actions were based on extracted hypotheses from observations (video-taped and analysed) of *Araneus* web-building behaviour. Surprisingly, for an accurate web simulation *Theseus* required no more than 13 simple rules controlling
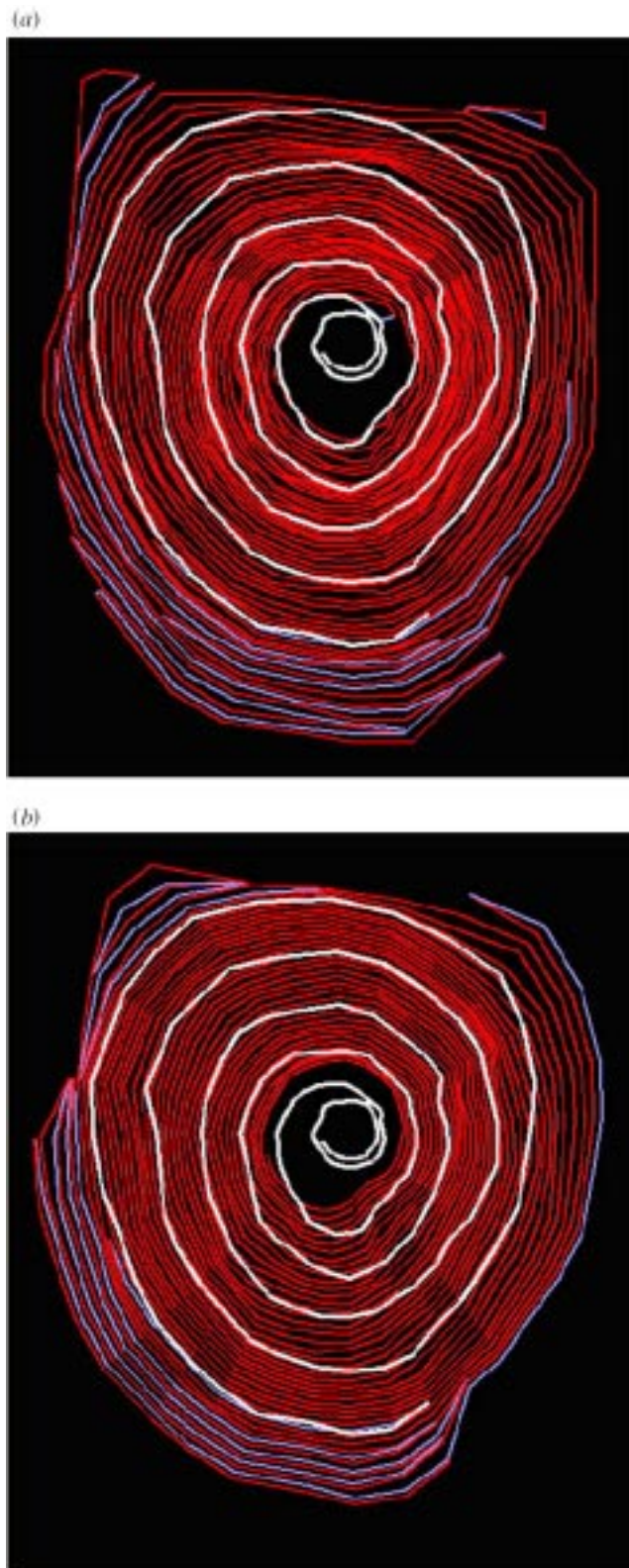
(a)

(b)

Figure 2. Example of matched coiling in real and virtual CSs. This figure shows the AS (white) and CS (red/blue) of a real web of *A. diadematus* (*a*), and a simulated web (*b*). The red threads indicate matched direction of coiling between the CS and AS, the blue threads show counter coiling. The percentage of matched coiling is calculated as the proportion of the total CS length where the AS and CS were built in the same turning direction (Zschokke 1993). All sampled values of this emergent property were found in a narrow range between 80 and 100%.
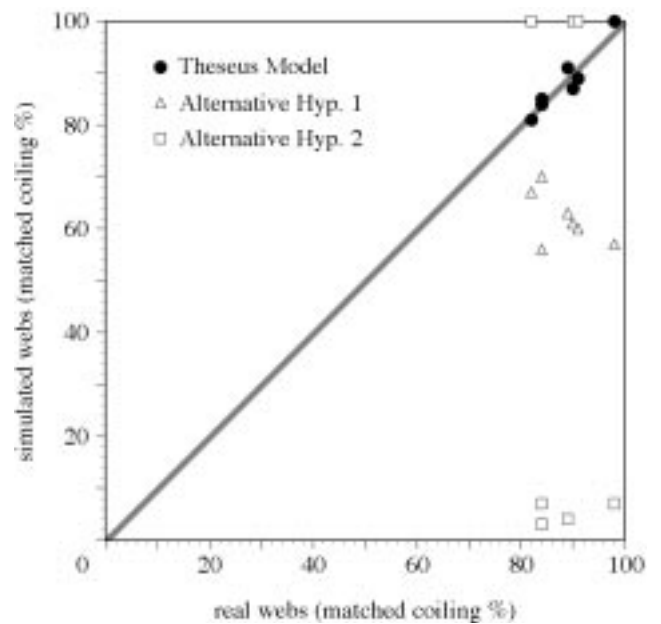
Figure 3. Comparison of matched coiling between real and virtual CSs. This figure shows a paired comparison of real (*x*-axis) and simulated (*y*-axis) web data. The percentage of matched coiling is the proportion of the total CS length where the AS and CS were built in the same turning direction. For our model, all sampled values of this emergent property were found in a narrow range between 80 and 100% (black circles). In contrast, two tested alternative hypotheses failed to mimic the emergent property (hypothesis 1, outlined triangles; hypothesis 2, outlined squares).

local action patterns (Krink & Vollrath 1998*b*). Figure 1 shows the effects of three basic rules on the construction of a CS thread. The rules and behaviour patterns were organized into three groups: (1) basic orientation and movement, mainly during (i) searching for radials or peripheral frame and spiral threads, (ii) orientation along the AS, and (iii) U-turn behaviour to maintain CS spacing; (2) web manipulations such as fixing new sticky threads and removing AS threads when they are no longer needed for support or orientation (the exact location of a joint is determined by a rule that compromises between (i) keeping a constant distance to the currently tracked auxiliary spiral thread, and (ii) keeping a constant distance between successive turns of the CS); and (3) gravity as a secondary spatial information cue for fine adjustments according to the spider's slower prey attack speed when running upwards.

For our comparison of emergent properties, each pair of webs constructed by *Araneus* and *Theseus* was digitized and analysed regarding the coiling pattern of its ASs and CSs. For this, we determined the length ratio of all CS threads that were built by the spider when following the coiling direction of the AS to all threads of the entire CS (matched coiling).

3. RESULTS

During the stage of CS construction, the cross spider *A. diadematus*, although on the whole tracking the coiling direction of the unidirectional AS, usually reverses several times the direction of its movement ($x = 9.86 \pm 1.97$ s.e., $n = 7$). The percentage of equal coiling of these spirals (matched coiling) depends upon the number and sequence of U-turns during the construction of the CS.

Surprisingly, the webs built by our virtual spider robot share this characteristic without any rule specifying any form of matching; this would indicate an emergent property (figure 2). We found little variance and no significant difference (paired t-test, $p = 0.853$, $n = 7$) for matched coiling in a paired comparison (figure 3, black circles) of real *Araneus* webs ($\bar{X}_r = 88.3\% \pm 2.1$ s.e.) and simulated *Theseus* webs ($\bar{X}_{h_0} = 88.1\% \pm 2.3$ s.e.).

Two rules were responsible for this observation of matched coiling. The first rule compromises between two distances: (i) spacing the CS segments (mesh size), and (ii) spacing the inner leg's hold on the AS to the outer leg's outreach for the capture thread attachment point. The second rule causes a U-turn if the latter of these distances has to be shortened owing to spatial constraints (i.e. owing to web frame asymmetry). The spider uses these rules repeatedly to transform the eccentric (initial) outer shape of the CS into a circular (final) inner shape while providing evenly spaced spiral segments. Because matched coiling is crucially dependent on the number and timing of U-turns, it surprised us that these two rules were sufficient to fully mimic the real garden cross spider without any instructions aiming to create this pattern. Indeed, any extra U-turn would markedly decrease coiling synchrony as reverses are typically few in number and much more frequent in the periphery of the web.

There are interesting alternative hypotheses for U-turn decisions. We tested the two most plausible ones but neither passed the test of matched coiling. The first hypothesis (figure 3, outlined triangles), based on angle measurements between radii and spiral threads (Vollrath & Mohren 1985; Eberhard 1988), failed significantly (paired t-test, $p < 0.001$, $n = 7$; $\bar{X}_{h_1} = 62.0\% \pm 1.9\%$ s.e.). The second (figure 3, outlined squares), based on spatial constraints of the frame (Peters 1948), resulted in either complete ($100.0\% \pm 0.0\%$ s.e., $n = 3$) or very low ($5.3\% \pm 1.0\%$ s.e., $n = 4$) matched coiling (overall, $\bar{X}_{h_2} = 45.9\% \pm 19.2\%$ s.e., $n = 7$), and thus failed to show compliance with real webs.

4. DISCUSSION

In the investigation presented, our virtual robot *Theseus* accurately mimicked a garden cross spider's local, elementary and repeated action patterns to generate the much more complex, global characteristics of a typical orb web. Because it emerged from an unpredictable self-organizing process, the corresponding geometric pattern of matched coiling in real and virtual webs strongly supports the validity of the decision rules which, although only in part, we and others previously deduced from observations and experiments (for reviews, see Peters 1954; Witt & Reed 1965; Witt *et al.* 1968; Shear 1986; Vollrath 1988, 1992; Eberhard 1990).

Indeed, emergent properties—such as matched coiling in this study—can be of general and great importance for behavioural research using individual-based artificial ethology modelling. Essentially, emergent properties are powerful criteria to judge how well a model explains the causes of complexity in a behaviour pattern. Thus, they are also good indicators for the animal's own rule system, its individual components and their interaction. We may assume that if *Theseus* builds a web with specific emergent

properties, so does *Araneus*. This allows us to further assume that the spider's web-building behaviour is so robust precisely because it consists of a few simple rules of thumb which, through their interaction in space and time, lead to the emergence of a complex structure. Most elegantly, such a system would be highly adaptable, since inhibiting or changing the weighting of only one of the many components would lead to a very different structure. Over phylogenetic time, spiders have evolved a wide range of web architectures (for review, see Shear 1986) and, over ontogenic time, spiders will respond to changes in their internal and external physiological state with short-term modifications in web engineering (for review, see Vollrath 1992). This demonstrates as much the flexibility of the spiders' web-building algorithm as the success of simplicity and interactivity in rules that generate complexity.

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